Mating Behavior in *Littorina planaxis* Philippi

(Gastropoda : Prosobranchiata)

BY

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(7 Text figures)

The habitat of the grey periwinkle, *Littorina planaxis* Philippi (1847), well above high water on rocky western North American shores, exposes this snail to desiccating sun and wind and high temperatures to a greater degree than most other intertidal organisms (Ricketts & Calvin, 1952). This degree of exposure presents several problems to the process of reproduction. Fertilization is internal, which requires that males must have some means of locating females, recognizing them as such, and mating with them. This paper will attempt to explore the mating behavior of *Littorina planaxis* and explain its method of locating other individuals, differences in the behavior of males and females, and the anatomy and mechanics of copulation.

Studies were made at Hopkins Marine Station, Pacific Grove, Calif., during April and May, 1964. Egg-laying and copulating individuals were seen throughout this period. Ricketts & Calvin (1952, p. 13) state that some individuals can be found copulating at any time of year, but spring and summer seem to be the times for heavy occurrences of mating.

LOCATING OF MATING PARTNERS

All movement and any subsequent locating of mating partners in *Littorina planaxis* occurs when the rocks on which these winkles are living are moist. This may be at night or at any time during the day, and may take place even in direct sunlight. Tide height and wave action are two of the main factors that govern rock wetness. Males and females follow mucus trails of other individuals over moist rock, with apparent disregard for the sex of the snail that laid down the trail they are following, using their cephalic tentacles to feel their way along (Peters, 1964). Such following of mucus trails has selective advantage, since it leads winkles to other winkles, which may be potential mating partners.

PAIRING BEHAVIOR

Males differ from females in that they immediately climb upon the shell of any other *Littorina planaxis* individual they encounter, usually over the head end of the shell and often after touching tentacles with the other snail. Once on the shell, the male will migrate to the right side and insert his penis into the mantle cavity of the snail beneath him, assuming the pairing position shown in Figure 1. This position is necessary for copulation, since the genitalia in both sexes are found on the right side, behind the head (for a complete illustration of Littorine anatomy, see Fretter and Graham, 1962, Chapter 2, pp. 14-48). When the animal below is a female, copulation may ensue. However, it appears that success or failure of the tip of the penis in contacting the bursa copulatrix of the female mantle cavity is the only way in which a male

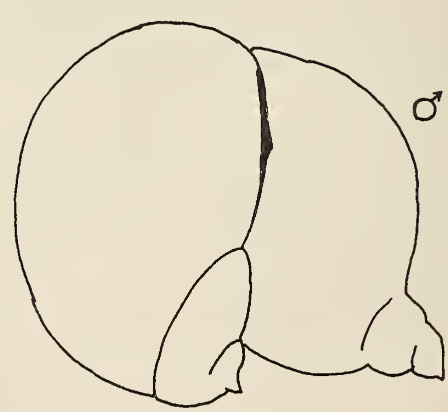

Figure 1: Pairing position, female from above, male from left side. Male's foot entirely attached to female shell, female clinging to substrate. (x 4)

can tell whether he has encountered a female or another male. A male exhibits no defensive reaction to having his mantle cavity explored by the penis of another male, but the male above will soon climb off and seek another mate if his probings do not meet with success. Observations were made of 32 males placed on a moist rock in the laboratory and watched for an hour and a half. No females were present. During this time, 12 pairs formed, and the length of time that each remained in the pairing position was recorded. None of the male-male pairs observed persisted for more than 8 minutes, and more than half of them broke up in two minutes or less. Because of their short duration, male-male pairs are not prevalent in the field at any one time. Parallel observations of 32 females in the absence of males under the above conditions yielded no pairing or climbing on one another's shells.

This apparent trial-and-error method of finding a mate could be of great selective advantage in the range where *Littorina planaxis* lives.

A male becomes aggressive if he comes into contact with another male on the shell he is exploring or intending to explore. Ten battles resulting from such circumstances have been observed, lasting between 30 seconds and 3 minutes, consisting of the males jerkily pushing each other with the head ends of their shells until one is dislodged. Figure 2 shows such a battle in progress.

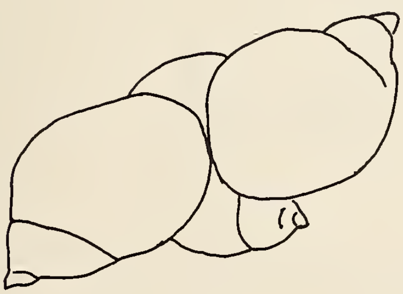

Figure 2: Mating battle, from above. The two males on the third snail will push each other until one is dislodged. This takes from thirty seconds to three minutes. (x 2)

In two cases, the snail, on which the fighting males were, was also a male, but they apparently did not know it, for the victor in each case attempted copulation with the snail beneath him.

Often a third snail will be found very close to or touching two paired individuals. In 50 checks of the sex of this third individual, 48 were found to be males, 2 females. The proximity of the second male to the pair might be due to his just having been pushed off the female, having not yet left the area, or it might suggest a chemo-attraction of males to the vicinity of females.

Laboratory and field studies showed, quite similarly, that normal (heterosexual) pairs persist for quite some time after formation, often spanning an entire moist-rock activity period of 10 hours or more. A field study of pair formation and persistence over one activity period is shown in figure 3. Pairs are seen to form over a wide range of dark and daylight hours, and are seen to persist for greatly varying lengths of time. A certain percentage of snails are to be found paired, with different partners, more than once during the same activity period as Figure 3 also shows.

The amount of pairing occurring at any time in the field seems to be affected by the level of the tide. Figure 4 shows two pairing frequency studies made over 25-hour tide cycles a week apart, demonstrating that the time shift in the tide level causes a concomitant shift in the time of day that the greatest and least numbers of individuals are paired. The area observed was about 1 meter square, containing about 100 *Littorina planaxis* individuals. Each hour the number of pairs and single winkles in the area was counted, the percentage pairing calculated, and plotted. The second week, as the tide came in later in the day, pairing percentage also peaked later. In both studies, pairing percentage rose as the tide came in, and then began to fall as the tide rose further. An increasing amount of splash, capable of dislodging paired snails, since in a pair only the female's foot is attached to the substrate, may account for this.

COPULATION

The trial-and-error behavior displayed by male *Littorina planaxis* in finding females suggests that copulation is the first purpose of pairing, and probably occurs immediately upon finding the female's genital opening. Figures 5a, b, & c illustrate insertion of the penis. It is first extended downward and backward, becoming engorged with blood and elongated (5a); as it continues to elongate, the front edge is pushed into the mantle cavity (5b); the tip trails in after the front edge and is eventually inserted in the bursa copulatrix (5c). Involuntary cilia in the penis cause a very rapid flow of sperm and prostatic secretions down the seminal groove that can be observed with a dissecting microscope. The rate of flow here makes it very unlikely that copulation takes very long, and it has been observed that sperm transfer is not always occurring during the entire time the penis is inserted. Of ten cases of copulation observed without disruption, the longest time the penis remained inserted was 15 minutes, more frequently only 4 or 5. The technique of observation was the collection of dry, closed pairs stuck together with mucus, which were then placed under seawater with the

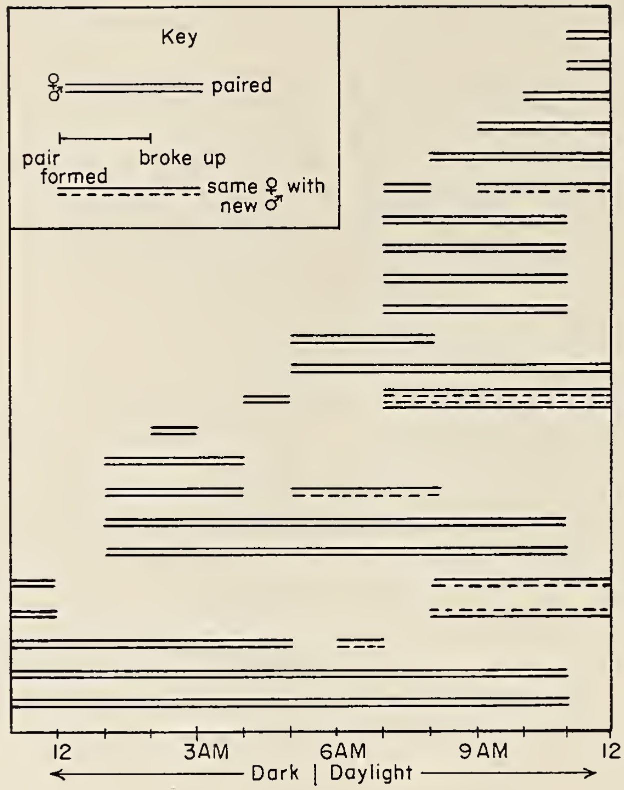

Figure 3: Record of field study of pair formation and persistence over one moist-rock activity period, showing that pairs form over a wide range of dark and daylight hours, and persist for greatly varying lengths of time. One individual may pair more than once during a single activity period.

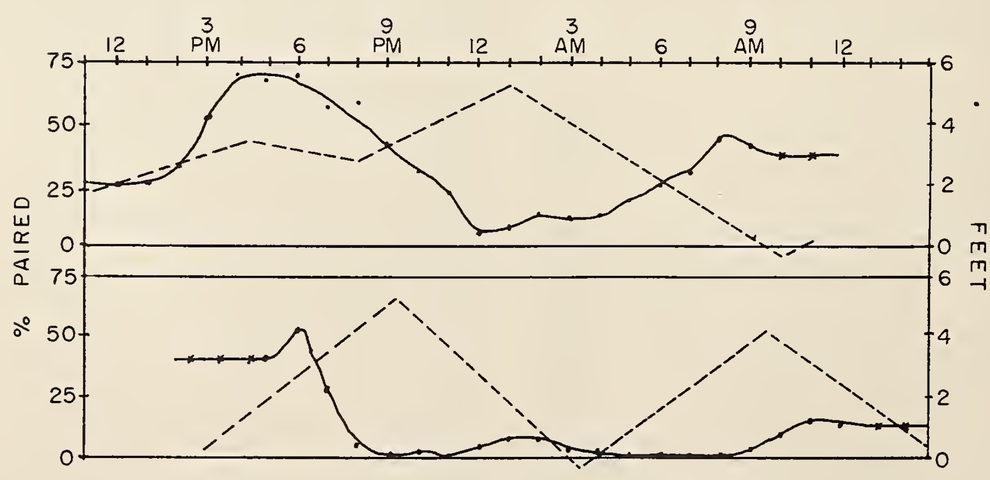

Figure 4: Two field studies of pairing percentage made over two 25-hour tide cycles one week apart, showing shifting of time of maximum and minimum pairing with tide-level time shift. See text for further explanation. ---- Tide level; ——— % paired. —×—×—× = % paired while snails are dry, drawn into shells, attached by mucus.

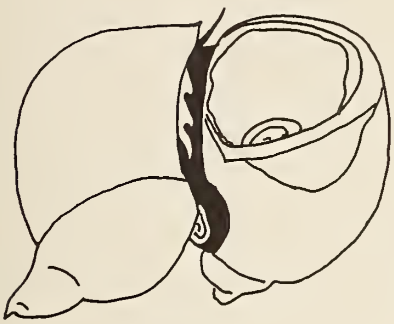

Figure 5 a

Figure 5 b

Figure 5 c

Figure 5 a: Pair, seen from below, with male extending penis down and back prior to insertion. Female with foot partially attached to glass plate, illustrating obstruction of view by subsequent spreading and flattening of foot. (x 2.5)

Figure 5 b: Male begins insertion of leading edge of fully extended penis into mantle cavity of female; the tip will trail in after. Fretter & Graham (1962) state that the mammaliform glands on the leading edge of the penis may produce secretions which aid in holding the penis in place during copulation.

Figure 5 c: Penis inserted as in sperm transfer. Female is waving foot about in an attempt to contact substrate in order to right herself.

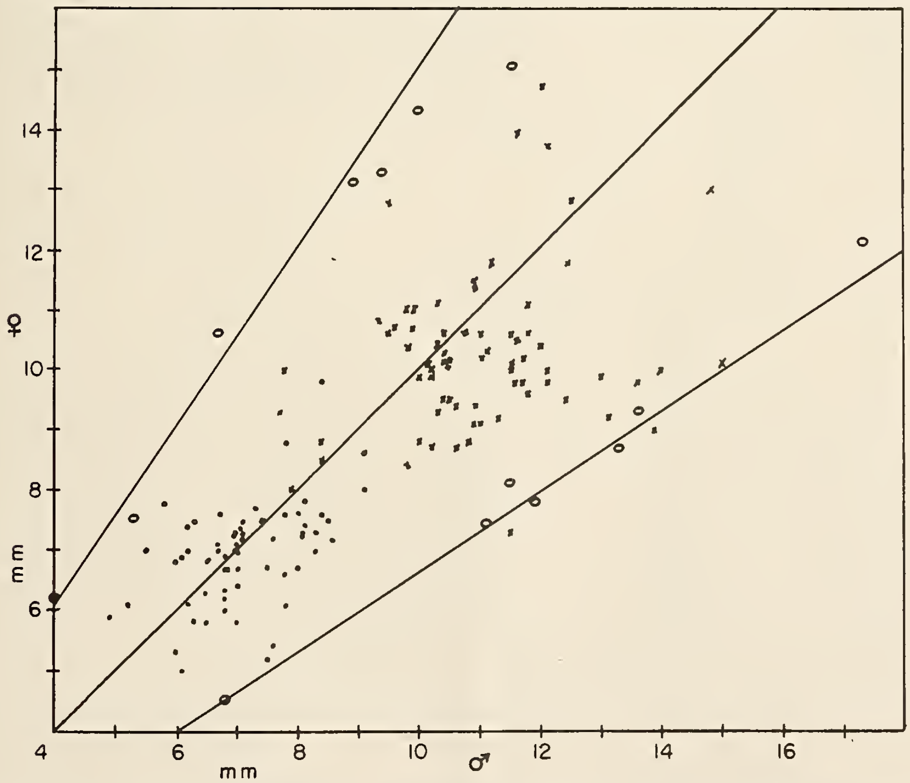

Figure 6

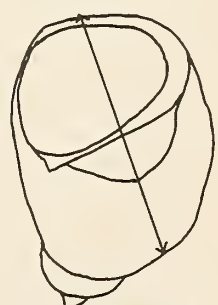

Figure 6 a

Figure 6: Scattergram of size of females plotted against size of males with whom they were paired. Two different populations and several pairs selected for their disproportion are represented. Each symbol between the diverging slope lines represents a pair in which the smaller member is at least $\frac{2}{3}$ the size of the larger • = population no. 1; 61 pairs. x = population no. 2; 72 pairs. o = the most disproportionate pairs found out of 84 pairs selected for this quality.

Figure 6 a: Method of measurement for Figures 6 and 7, across operculum and columella, from center of aperture lip to widest part of whorl opposite.

female on her back. Under these conditions the snails soon extended themselves, and the male usually attempted to insert the penis. The only drawback to this method of observation is occasional disruption of copulation as the female swings her foot around, trying to find a substrate in order to right herself. An attempt was made to avoid this problem by allowing the female to contact a glass plate with her foot while upside down; however, contact with the plate was followed by a spreading and flattening of the foot, which obscured the view of the penis and the female's mantle cavity.

When the female is righted, the position of the male shell during pairing completely obstructs the view of the penis. Since it is impossible to tell by male shell orientation whether or not the pair is copulating, field studies of duration or frequency of copulation are practically impossible. Disruption of 100 active (extended) pairs in the field revealed only 17 in which the male's penis was extended, so paired snails cannot always be regarded as copulating.

SIZE RATIOS IN MALE-FEMALE PAIRS

A question arises as to what size males will be found paired with what size females in the field, and whether any selection for size of mate occurs. Figure 6 is a scattergram of all the pairs of two different *Littorina planaxis* populations taken from two different areas, in which the size of each female is plotted against the size of the male she was paired with. The method of measurement used for both Figures 6 and 7 is shown in Figure 6a. All symbols between the diverging slope lines in Figure 6 represent pairs in which the smaller member is at least ⅔ the size of the larger. This suggests itself to be the practical limit in size disproportion in pairs found in the field. An overall survey of populations in which only the most disproportionate pairs were selected yielded only 4 out of 84 pairs taken that failed to fall within the suggested limits. A few of these limit-defining pairs are also recorded on the scattergram.

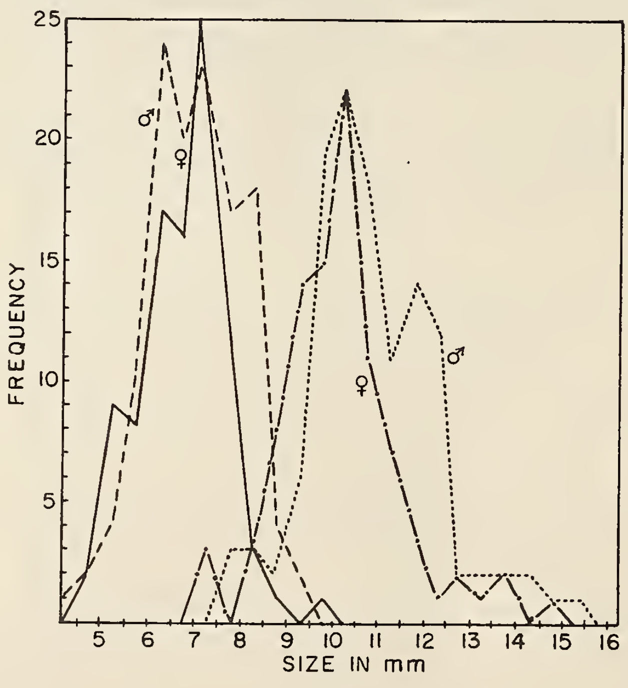

Figure 7: Size frequency by sex in populations 1 and 2 (see Figure 6). All individuals in each ½ mm category are plotted as one point, as there are 14 males between 11.5 mm and 12.0 mm.

——— = population 1; (93) females   – – – – = population 1; (126) males
–·–·– = population 2; (96) females;   ·········· = population 2; (120) males

A breakdown of size frequency by sex of the two scattergram populations is presented in Figure 7. Here is suggested one reason why more disproportionate pairs are not found: very large males and females are not found in the same populations with very small individuals. Therefore, in addition to the mechanical problems of copulation between *Littorina planaxis* individuals with grossly disproportionate genitalia, there are undoubtedly many ecological pressures involved which keep large and small snails apart in nature, such as size as a factor in withstanding wave shock, desiccation, etc. However, laboratory experiments in which large males were kept isolated with small females, and conversely, for two weeks yielded only one pair, barely exceeding the ⅔ limit, while evenly sized snails under the same environmental conditions paired readily and often.

SEX RATIO

As Figure 7 indicates, there are generally more males than females in the population. A survey of 100 unpaired individuals yielded a ratio of two males to each female: however, when the population as a whole and the large number of snails that are pairing at any one time are considered, the balance between the sexes is seen to be such that there is probably little or no significance in the greater number of males present.

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Macroscopic Algal Foods of *Littorina planaxis* Philippi and *Littorina scutulata* Gould

(Gastropoda : Prosobranchiata)

BY

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The upper littoral periwinkles of the central California coast are often found in association with a number of the higher intertidal macroscopic algae. The studies and observations upon which this paper is based were made on the Monterey Peninsula, on the central California coast, especially at Mussel Point in the vicinity of the Hopkins Marine Station, and at Pescadero Point. The coastline in these areas consists principally of granite boulders and outcroppings interspersed with sandy beaches, heavily overgrown with larger algae through most of the littoral zone. Observations were made during May, 1964, and therefore do not reflect any seasonal fluctuations that might take place.

Despite the fact that both *Littorina planaxis* Philippi, 1847 and *L. scutulata* Gould, 1849 are a conspicuous part of the upper littoral fauna over much of the Pacific coast of North America, almost nothing has been published about them up to now, and while the eastern United States and European periwinkles are generally better known, information on food and feeding patterns is very scarce. North (1954) analyzed size distribution, erosive activities, and gross metabolic efficiency of both *L. planaxis* and *L. scutulata*. Castenholz (1961) used *L. scutulata* as well as *Acmaea* spp. in his studies of grazing effects on diatom populations. From his observations, he assumed "that the primary food of these gastropods is diatom material" (p. 793), with blue-green algae the principal food in the "supra-littoral" fringe. Ricketts & Calvin (1952) state that *L. planaxis* feeds on detritus and microscopic plants scraped from almost bare rock, and that "certain of the rockweeds *(Pelvetia* or *Fucus)* serve the young periwinkles as a sort of nursery, for it is on their fronds and stems that the young will nearly always be found" (p. 20), an observation for which no evidence has